Estimating the diversity of arboreal oonopid spider assemblages (Araneae, Oonopidae) at Afrotropical sites

Wouter Fannes, Domir De Bakker, Katrijn Loosveldt and Rudy Jocqué: Invertebrate Section, Department of African Zoology, Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium. E-mail: wouter.fannes@africamuseum.be

Abstract. The abundance, species richness, and assemblage structure of arboreal Oonopidae of Afrotropical rainforests and savannahs was investigated. Canopy-dwelling spiders were collected by insecticide knockdown fogging at 11 rainforest and three savannah sites in West, Central, and East Africa. In two lowland rainforests (Luki, DR Congo, and Kakum, Ghana) and two savannahs (Faro, Cameroon, and Mkomazi, Tanzania) Oonopidae were the second most abundant spider family, comprising up to 22% of the arboreal arachnofauna. In total, 51 species and 11 genera of Oonopidae were recorded from the 14 study sites. Kakum was the most species- and genus-rich site, with 11 species and 5 genera recorded. The arboreal oonopid assemblages were almost invariably found to be dominated by the widely-distributed genera *Orchestina* Simon and *Opopaea* Simon, in terms of both abundance and species richness. *Orchestina* in particular can be highly abundant and can comprise more than 90% of arboreal oonopids in rainforests as well as in savannahs. Species accumulation curves and six nonparametric estimators of total species richness (Chao 1, Chao 2, ACE, first- and second-order jackknife, and bootstrap) were calculated for Luki, Kakum, and Faro to evaluate the level of inventory completeness. In Kakum and Faro the species accumulation curve respectively closely approached and reached a stable asymptote. The selected nonparametric estimators were found to lack predictive power when applied to the Faro data set and appeared to behave similarly poorly on the Kakum sample set.

Keywords: Goblin spiders, Planetary Biodiversity Inventory, rarefaction, tree crowns, eeology

The Oonopidae (goblin spiders) are a worldwide family of very small spiders whose diversity, phylogeny and ecology remain poorly known. In major spider compendia (e.g., Dippenaar-Schoeman & Jocqué 1997; Song et al. 1999; Ubick et al. 2005) and in papers on their taxonomy and biology (e.g., Saaristo & van Harten 2002; Burger 2007) oonopids are usually treated as being mainly restricted to the ground layer. Yet, this prevailing view on the vertical distribution of the family may be in need of revision as several canopy survey studies published since 1990 have demonstrated the presence of oonopids in the radically different environment of tropical forest canopies (Table 1 summarizes this literature). At some sites Oonopidae were even reported to constitute a major component of the arboreal arachnofauna in terms of abundance, accounting for up to 17% of all adult spiders collected (Sorensen 2004).

Despite the increasing number of reports, current knowledge of arboreal oonopid assemblages can still only be described as rudimentary since even primary, descriptive data is largely lacking. Perhaps most notable in this regard is the paucity of data on the morphological diversity of canopydwelling Oonopidae. Although a majority of the aforementioned studies have recorded species numbers, only two (Russell-Smith & Stork 1994, 1995) have provided genus-level identifications of the oonopid fauna.

In this study we present data on the abundance, species richness, and generic affinities of canopy-inhabiting Oonopidae at 14 Afrotropical rainforest and savannah sites. In addition, species accumulation curves and several nonparametric estimators are used to estimate total species richness of arboreal oonopid assemblages at three of these sites.

METHODS

Study sites.—Canopy spiders were collected by insecticide knockdown fogging at 14 sites in West, Central, and East Africa. Figures 1a-b show the location of all study sites.

Details on the localities Luki, Kakum, and Faro are given below, while characteristics of the other study sites are listed in Table 2; additional information on Kakamega, Budongo, Cyamudongo, Ibanda Makera, Mkomazi, and Comoé can be found in Freund (2005), Wagner (1997, 2003), Krüger & McGavin (1997), and Mody et al. (2003).

Luki Biosphere Reserve (05°37′S, 13°06′E) is situated in the Bas-Congo region of the DR Congo and consists of lowland rainforest. Annual rainfall averages 1120 mm, with a single wet season usually lasting from mid-October to mid-May. Fog days average 164 per year. Five primary forest samples were taken at an elevation of about 266 m between 4 and 13 November 2006.

Kakum National Park (05°21′N, 01°23′W) is situated in the Central Region province of Ghana and consists of adjacent plots of primary and 40 year-old secondary rainforest. Rainfall averages 1500–1800 mm per year and is bimodal, with wet seasons between March–July and September–November. Twelve samples (six from primary and six from secondary forest canopy) were taken at an elevation of about 159 m between 12 and 25 November 2005.

Faro Game Reserve (08°24′N, 12°49′E) is located in northern Cameroon and consists of wooded savannah and gallery forest. Average annual rainfall is 500–1000 mm. Ten gallery forest trees and nine savannah trees were sampled at an elevation of about 300 m between 18 April and 3 May 2007, at the beginning of the local wet season (May–October).

Collecting methods.—We used the following fogging protocol in Luki, Kakum, and Faro. On each sampling occasion a SWINGFOG SN 50 fogger (Swingtec GmbH) was operated from the ground for 6 (Faro) or 10 (Luki, Kakum) minutes, generating an insecticidal fog from a 1% solution of natural pyrethrum in diesel. Arthropods were collected on triangular or rectangular sheets with a combined area of about 64 (Luki, Kakum) or 72 (Faro) square meters. Sheets were suspended

Table 1.—Overview of published data on the abundance and species richness of Oonopidae in tropical and subtropical forest canopies. * denotes studies that included juvenile spiders. Rank: rank of Oonopidae among all spider families present at

	Reference	1/28 Sørensen 2004	37 Silva 1996	30 Silva 1996	? Höfer et al. 1994	Floren & Deeleman-Reinhold 2005	22 Russell-Smith & Stork 1995*	? Russell-Smith & Stork 1994*	14 Russell-Smith & Stork 1994*		7/19 Basset 1990, 1991	? Guilbert et al. 1994*	? Guilbert 1997*	? Guilbert 1997*
ae	Rank	11/2	113	02/9		12/29	7/22		4/14		1/2			
Oonopidae	%	2.0	3.6	5.1	ç	1.2	2.1	ć	10.0		2.8	ç.	ċ	i
1	Spp.	3	30	34	ċ	7	4	ċ	2		2	ċ	ċ	i
Total spider	spp.	149	844	673	ن	578	190	٤	50		72	i	ć	i
13	Rank	2/28	5/37	6/30	3/16	7129	9/22	8/19	4/14		8/19	5/11	4/17	4/17
Oonopidae	%	16.9	6.7	5.1	14.8	3.9	2.4	3.8	11.0		9.0	3.8	9.7	4.9
0	Ind.	884	394	73	12	272	23	46	48		∞	188	512	78
Total Spider	Indivs.	5233	4068	1427	81	6669	945	1211	438		1408	4947	8929	1594
	Habitat	rainforest	rainforest	rainforest	rainforest	rainforest	rainforest	rainforest (lowland)	rainforest	(submontane)	rainforest	sclerophyll forest	sclerophyll forest	rainforest
	Study site	Uzungwa, Tanzania	Samiria River, Peru	Tambopata-Candamo, Peru	Reserva Adolpho Ducke, Brazil	Kinabalu/Crocker Range, Borneo	Ladan Hills, Borneo	Dumoga-Bone, Sulawesi	Dumoga-Bone, Sulawesi		Mt. Glorious, Australia	Mt. Nondoué, Païta, New Caledonia	Pindaï, New Caledonia	Rivière Bleue, New Caledonia

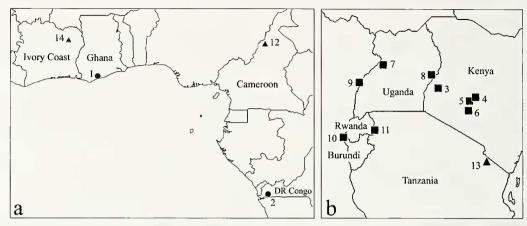
1.5 m above the ground. In Faro, individual trees were fogged while in Luki and Kakum selected areas (10–15 m high) of the closed canopy were targeted. After a drop time of 2 hours, specimens were concentrated by brushing and subsequently stored in 70% (Luki, Kakum) or absolute (Faro) ethanol. Sampling usually took place at dawn when wind speeds were lowest. In Luki the first fogging was disturbed by severe fog scatter. The same patch of canopy was refogged 18 hours later when weather conditions were more favorable. As these two foggings yielded a combined number of oonopids comparable to most undisturbed samplings, they were merged and counted as a single sample (first sample in the species-by-sample matrix, see below). Understorey vegetation was avoided or, when possible, cleared. The other 11 sites were sampled by W. Freund (Kakamega), G. McGavin (Mkomazi), K. Mody (Comoé), and T. Wagner (Kakamega, Mt Kenya, Aberdare, Gatamayu, Budongo, Mt. Elgon, Semliki, Cyamudongo, and Ibanda Makera) between October 1993 and January 2003. Details on the fogging protocols used at these sites can be found in the references given in Table 2.

Morphotyping.—All adult spiders collected were identified to family level and sorted to morphospecies. Subsequently, the generic affinities of all oonopid morphospecies were determined. When morphospecies could not be accommodated in one of the 73 currently described genera (Platnick 2008) they were assigned to morphogenera coded undescribed genus 1, 2, 3 etc. In order not to artificially inflate species and genus counts, a conservative approach was applied to delimiting morphospecies and morphogenera (henceforth referred to as species and genera). The material is deposited in the Royal Museum for Central Africa in Tervuren, Belgium (Luki, Kakum, and Faro), the Oxford University Museum of Natural History in Oxford, UK (Mkomazi), and the Alexander Koenig Museum in Bonn, Germany (other sites).

Comparison of subhabitats.—In both Kakum and Faro two distinct subhabitats were sampled. A two-sample t-test was applied to the Kakum data to check for differences in oonopid abundance and species richness between primary and secondary forests. Hierarchical cluster analyses were then performed to evaluate whether these forest types differed markedly in community composition. First, we calculated four different indices of compositional similarity viz. the incidence (presence/ absence)-based classic Jaccard and Sorensen indices and the abundance-based Bray-Curtis and Morisita-Horn indices. Four dendrograms were subsequently generated from each similarity matrix by implementing four different joining algorithms viz. single linkage (nearest neighbor), complete linkage (furthest neighbor), centroid linkage, and Ward's method. The 16 resulting dendrograms were then inspected to assess the level of clustering among samples from the same forest type.

As data deviated significantly from normality (Shapiro-Wilk test, P < 0.01), the nonparametric Mann-Whitney U statistic was used to test for significant differences in oonopid abundance between gallery forest and savannah trees at Faro. Differences in species richness and community composition were evaluated as outlined above.

The comparisons between subhabitats constitute comparative mensurative experiments (Hurlbert 1984). In order to reduce the risk of pseudoreplication sensu Hurlbert (1984) we



Figures 1a, b.—Location of study sites. a. Kakum (1), Luki (2), Faro (12) and Comoé (14); b. Kakamega (3), Mt. Kenya (4), Aberdare (5), Gatamayu (6), Budongo (7), Mt. Elgon (8), Semliki (9), Cyamudongo (10), Ibanda Makera (11) and Mkomazi (13). ● lowland rainforest ■ montane forest ▲ savannah.

selected trees (or areas of canopy) that were dispersed throughout the subhabitat. A single sample was taken from each tree or area of canopy.

Total oonopid species richness.—For Luki, Kakum, and Faro the exact composition of each individual sample taken is

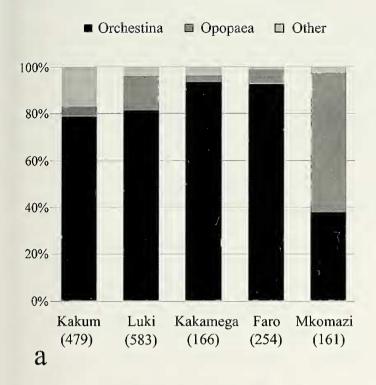
known. This allowed us to estimate the total oonopid species richness at these sites and to evaluate the completeness of our censuses. For this purpose species accumulation curves (also called sample-based rarefaction curves, Gotelli & Colwell 2001) were calculated analytically ("Mao Tau," Colwell et al.

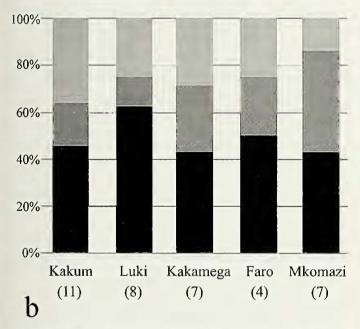
Table 2.—Habitat and sampling details for 11 of the 14 study sites (see Methods section for details on Luki, Kakum, and Faro).

		Sampling						
Study site	Habitat	No. of samples	Season	Fogging protocol				
Kakamega Forest, Kenya	prim./sec. forest	200	wet/dry	Wagner 2003, Freund 2005				
Mt. Kenya, Kenya	prim. rainforest	19	dry	Wagner 2003				
Aberdare, Kenya	prim. rainforest	8	dry	Wagner 2003				
Gatamayu, Kenya	prim. rainforest	23	dry	Wagner 2003				
Budongo Forest, Uganda	prim./swamp/sec. forest	103	wet/dry	Wagner 2003				
Mt. Elgon, Uganda	prim, rainforest	8	dry	Wagner 2003				
Semliki Forest, Uganda	prim. rainforest	24	dry	Wagner 2003				
Cyamudongo, Rwanda	sec. rainforest	9	wet	Wagner 1997				
Ibanda Makera, Rwanda	gallery/dry forest	7	wet	Wagner 1997				
Mkomazi, Tanzania	semiarid savannah	31	dry	Krüger & McGavin 1997				
Comoé, Ivory Coast	Guinea-savannah	31	wet	Mody et al. 2003				

Table 3.—Abundance and species richness of arboreal Oonopidae at 14 Afrotropical rainforest (lowland and montane) and savannah sites. s %: percentage of singletons. Rank: rank of Oonopidae among all spider families present at a site.

		Total spider		Oonopida	e	Total spider	Oonopidae				
Study site	Habitat	indivs.	Ind. %		Rank	spp.	Spp.	%	Rank	s %	
Kakum, Ghana	lowland	4587	479	10.4	2/27	297	11	3.7	6/27	9.1	
Luki, DR Congo	lowland	3545	583	16.4	2/26	231	8	3.5	8/26	12.5	
Kakamega, Kenya	montane	3452	166	4.8	6/29	367	7	1.9	9/29	28.6	
Mt. Kenya, Kenya	montane	1957	60	3.1	5/21	85	7	8.0	4/21	14.3	
Aberdare, Kenya	montane	1136	15	1.3	9/16	42	4	9.5	4/16	25	
Gatamayu, Kenya	montane	1082	65	6.0	4/20	79	4	5.1	5/20	0	
Budongo, Uganda	montane	2844	89	3.1	7/24	422	7	1.7	9/24	14.3	
Mt. Elgon, Uganda	montane	2516	137	5.4	3/13	33	3	9.1	3/13	0	
Semliki, Uganda	montane	276	29	10.5	3/16	122	3	2.5	8/16	33.3	
Cyamudongo, Rwanda	montane	198	9	4.5	6/16	67	2	3.0	7/16	0	
Ibanda Makera, Rwanda	montane	117	4	3.4	8/12	54	2	3.7	7/12	50	
Faro, Cameroon	savannah	1162	254	21.9	2/18	96	4	4.2	6/18	0	
Mkomazi, Tanzania savanna		1078	161	14.9	2/18	196	7	3.6	6/18	14.3	
Comoé, Ivory Coast	savannah	764	12	1.6	9/17	125	1	0.8	12/17	0	





Figures 2a, b.—Relative abundance and species richness of *Orchestina*, *Opopaea*, and other genera at the five study sites where >150 Oonopidae were collected. a. Relative abundance (total oonopid abundance is given in brackets for each site); b. Relative species richness (observed oonopid species richness in brackets).

2004). In addition, six nonparametric richness estimators were plotted using 200 randomizations (without replacement) of sample accumulation order. Nonparametric estimators assess "true" richness from the distribution of rare or infrequent species and are considered the most promising and potentially most powerful approach to estimating the total species richness of communities (Gotelli & Colwell 2001; Magurran 2004), usually outperforming other methods such as curve-

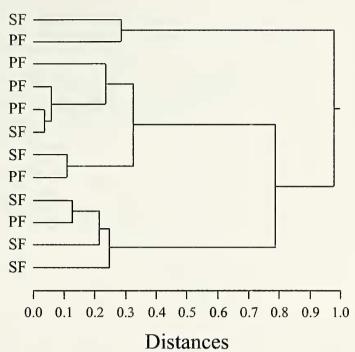


Figure 3.—Dendrogram (Morisita-Horn index/complete linkage) of primary forest (PF) and secondary forest (SF) samples taken at Kakum.

fitting (Walther & Moore 2005). The estimators selected were the abundance-based Chao 1 and ACE and the incidence-based Chao 2, bootstrap and first- and second-order jackknife (henceforth Jack 1 and Jack 2). The bias-corrected forms of Chao 1 and 2 were used. Because the collecting protocol applied in Luki, Kakum, and Faro resulted in large but relatively few samples the ICE estimator was not selected. The Coleman-curve was also calculated for each site. Computation of individual-based rarefaction curves such as the Coleman-curve assumes random mixing of individuals and the difference between a species accumulation curve and the corresponding Coleman-curve therefore serves as a measure of patchiness (Colwell & Coddington 1994).

Similarity indices, rarefaction curves and estimators were calculated using EstimateS version 8.0.0 (Colwell 2006). SYSTAT version 12 was used for statistical analyses and hierarchical clustering. Further details on rarefaction curves and on the similarity indices and nonparametric estimators used in this study are provided by Gotelli & Colwell (2001), Magurran (2004) and on the EstimateS website (Colwell 2006). Species-by-sample abundance matrices for Luki, Kakum, and Faro are available online at http://www.africamuseum.be/research/zoology/invertebrates/index_html in EstimateS Format 1.

RESULTS

Abundance and diversity of arboreal Oonopidae.—Our data on the relative importance of Oonopidae as a component of arboreal spider faunas are presented in Table 3. In both lowland rainforests oonopids rank second in abundance only to the Theridiidae, accounting for 10.4% in Kakum and 16.4% in Luki. In two out of three investigated savannah sites, oonopids also rank second in terms of abundance (in both

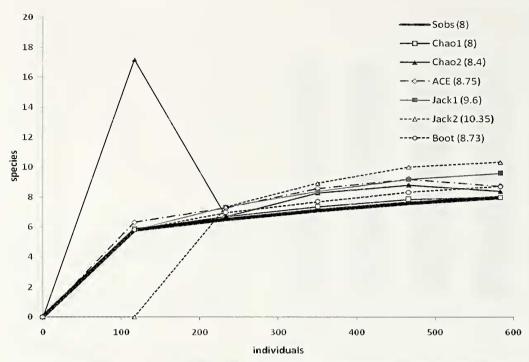


Figure 4.—Species accumulation curve (Sobs) and nonparametric estimator curves for Luki. Final values in brackets. Boot = bootstrap.

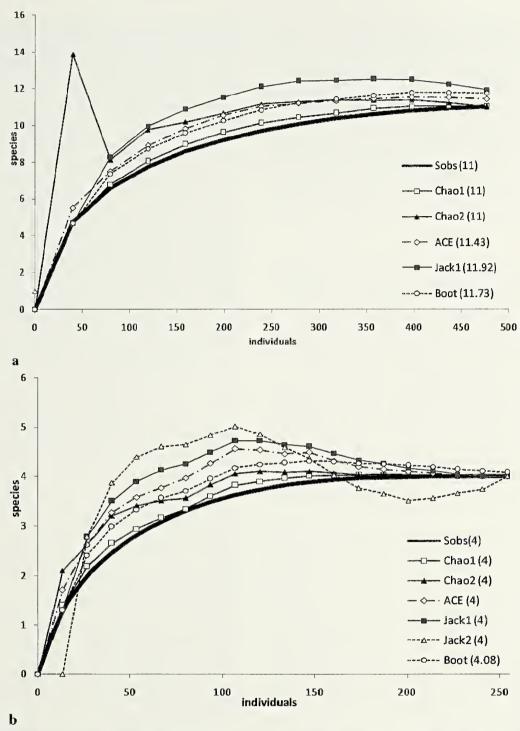
cases again after theridiids), contributing 14.9% in Mkomazi and 21.9% in Faro. Oonopidae usually comprise a small proportion of total spider species richness but they do contribute substantially (more than 9%) to the relatively species-poor arboreal arachnofaunas of some montane forests (Aberdare, Mt. Elgon). The lowland rainforest of Kakum emerges as the most speciose and genus-rich site, with 11 species and 5 genera of Oonopidae observed. Species richness in savannah habitats varies from low (only 1 species in Comoé despite considerable sampling efforts, see Mody et al. 2003) to relatively high (seven species in Mkomazi, equalling or exceeding the observed richness in most investigated rainforest sites). The relatively low proportion of species represented by a single individual (singletons; Table 3) can be taken as an indication that the arboreal oonopid assemblages have been sampled representatively at most study sites.

The 2063 adult Oonopidae collected from the 14 study sites belong to 51 species and 11 genera. A high proportion of the inventoried genera (73%) are presently undescribed. The genus Opopaea Simon 1891 was recorded in all sites while Orchestina Simon 1882 occurred in seven rainforest and two savannah sites. Most other genera were recorded from only one or two sites (Appendix 1 gives a complete overview of the species collected at each site). Of the total number of collected oonopids Orchestina makes up 67.4% and Opopaea 22.8%. All other genera contribute very little, with undescribed genus 4 being the most abundant (3.7%). Orchestina and Opopaea comprise 35.3% and 33.3%, respectively, of the total number of recorded species, with undescribed genus 1 ranking third (7.8%). The dominance of *Orchestina* and *Opopaea* also holds when individual study sites are considered, as these two genera account for most of the oonopid abundance and species richness at almost every site (Figs. 2a, b). Orchestina in particular can be highly dominant, as exemplified by the study sites Luki, Kakum, Kakamega, and Faro (Fig. 2a).

Comparison of subhabitats.—In Kakum, primary and secondary forest samples did not differ significantly in oonopid abundance (t-test, P=0.85) or species richness (t-test, P=0.88). The 16 dendrograms that were generated exhibited considerable differences in topology. However, primary and secondary forest samples did not form separate clusters within any of these trees but instead were almost completely interspersed throughout each dendrogram (Fig. 3). A similar lack of differentiation between primary and secondary forest assemblages was found in most other spider families present in Kakum (own unpublished data) and may arise primarily from the close adjacency of both forest types, which permits ready recolonization of the regenerating secondary forest.

Gallery forest trees and savannah trees in Faro did neither differ significantly in abundance (Mann-Whitney test, P = 0.65) nor in species richness (t-test, P = 0.79). As in Kakum, the cluster analysis dendrograms lacked any resolution for subhabitat type. Both the Faro and Kakum data sets are, therefore, analyzed as a whole in the following section.

Estimation of total oonopid species richness.—In Luki (eight observed species; Fig. 4) the species accumulation curve continues to rise as sample number increases without showing signs of approaching an asymptote. The Chao 1 estimator curve closely resembles the empirical curve but appears to level off at high sample numbers. ACE and Chao 2 estimates begin to fall as the maximum number of samples is approached. The Jack 1, Jack 2, and bootstrap curves on the other hand, continue to rise in parallel with the species accumulation curve. This lack of consensus among estimators is echoed in their total richness estimates, which do not cluster tightly but range from 8 (for Chao 1) to 10.35 (Jack 2). Taken together, these results do not provide clear evidence that the inventory at Luki was nearing completeness and sustained collecting efforts may therefore result in many as yet unseen species.



Figures 5a, b.—Species accumulation curves (Sobs) and nonparametric estimator curves for Kakum and Faro. a. Kakum; b. Faro. Final values in brackets. Boot = bootstrap.

In Kakum (11 observed species; Fig. 5a), the species accumulation curve approaches a stable asymptote as the maximum number of samples is reached. Of the estimators tested, only Jack 2 fails to provide a reasonable estimate as it generates a total species richness estimate (10.48) that is lower than the observed number of species (see Sørensen 2004 for another example of this behavior); it is therefore not presented in Figure 5a. All other estimator curves start to decline as the maximum number of samples is approached and finally

converge closely on the observed richness, with estimates ranging from 11 (for Chao 1 and Chao 2) to 11.92 (for Jack 1).

In Faro (four observed species; Fig. 5b) the species accumulation curve reaches a stable asymptote. This condition eliminates the need for nonparametric estimators but at the same time allows for a direct and rigorous test of their performance (Gotelli & Colwell 2001). As in Kakum, the Jack 2 estimator performs least satisfactorily, generating an erratic curve which is still climbing steeply at its end point. The other

estimator curves level off as increasingly more samples are pooled and finally stabilize at an estimate of 4 species, with the exception of the bootstrap curve which continues to decline slowly and gives a final estimate of 4.08. However, none of the estimators stabilizes sooner than the species accumulation curve.

No evidence for a strong departure from the assumption of homogeneity (Colwell & Coddington 1994) was found, the species accumulation eurves lying at most 0.25 (Luki), 1.01 (Faro), and 2.15 (Kakum) standard deviations (SDs) below their corresponding Coleman-curves (for comparison, the seed bank data set of Colwell & Coddington (1994) gives a maximum difference of 1.7 SDs). The near-identity of the empirical and Coleman-curves in Luki indicates a very low level of patchiness.

DISCUSSION

The first quantitative data on arboreal Oonopidae of the Afrotropical region were provided by Sorensen (2004), who reported that oonopids accounted for almost 17% of the canopy spiders in a Tanzanian montane forest. In the present study, similarly high abundances are recorded from lowland rainforests and even from savannahs. Furthermore, it is shown that arboreal oonopid assemblages can be both speciose and genusrich. Despite their often considerable morphological diversity, assemblages were invariably found to be dominated by either *Opopaea* or *Orchestina*. The dominance of the latter genus, in particular, can be very pronounced and is not geographically restricted to the African tropics, as *Orchestina* also dominates canopy-dwelling oonopid faunas on Borneo (C. Deeleman, pers. comm.) and Sulawesi (A. Russell-Smith, pers. comm.).

Calculation of species accumulation curves showed that our inventory at Faro was essentially complete and the 4 species and 3 genera collected at this savannah site thus very likely represent the entire oonopid fauna that is accessible to the fogging method and present as adults at the beginning of the rainy season. Similarly, the 11 species and 5 genera collected at Kakum were shown to represent a nearly complete inventory of the arboreal oonopid assemblage of this lowland rainforest.

Although the selected nonparametric estimators all converged very closely on the observed richness when applied to the Faro data set, none reached a stable asymptote sooner than the species accumulation curve (one of the most desirable properties of a good estimator, Gotelli & Colwell 2001) and all estimators were thus devoid of any predictive power. When judged against this asymptote criterion, the estimators also seem to perform poorly on the Kakum sample set, as none of the plotted estimator curves appears to approach an asymptote much faster than the empirical curve.

As a consequence of our and Sørensen's surveys in Africa, assemblage structure is now better known for canopy-dwelling Oonopidae than for their ground-living counterparts, a rather unusual state of affairs for a tropical spider family. Yet, many important questions remain to be addressed. One of these concerns the extent of seasonal changes in arboreal oonopid assemblages. These may be considerable, as indicated by the large seasonal fluctuations in oonopid abundance recorded in two New Caledonian forests (E. Guilbert, pers. comm.). Perhaps most urgently needed, however, are studies that investigate the level of vertical stratification of oonopid communities by comparing the canopy- and ground-dwelling

faunas of a single site with regard to their species composition. Recent pitfall trapping in primary forest in Luki (November 2006 and September-October 2007) suggests that oonopid communities can be strongly vertically stratified, as only one of the seven species collected at ground-level also occurs in the canopy (own unpublished data). The knowledge gained by studies addressing vertical stratification and seasonal variation can in turn be used to manage eollection resources for the ongoing Planetary Biodiversity Inventory project on this spider family (www.research.amnh.org/oonopidae).

ACKNOWLEDGMENTS

This study was supported by the National Science Foundation's Planetary Biodiversity Inventory project "The Megadiverse, Microdistributed Spider Family Oonopidae" and the Belgian Federal Science Policy. Additional financial support was provided by the Leopold III foundation. Two anonymous reviewers and ecology editor Søren Toft provided valuable comments on the manuscript. We thank Y. Basset, C. Deeleman, W. Freund, E. Guilbert, B. Huber, M. Leponce, G. McGavin, K. Mody, A. Russell-Smith, D. Silva, and T. Wagner, for providing material and/or information and M. Alderweireldt, L. Baert and J.-P. Michiels for assistance in the field. The first two authors contributed equally to this work.

LITERATURE CITED

Basset, Y. 1990. The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging; composition of the fauna. The Entomologist 109:173–183.

Basset, Y. 1991. The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. Australian Journal of Zoology 39:171–190.

Burger, M. 2007. Sperm dumping in a haplogyne spider. Journal of Zoology 273:74-81.

Colwell, R.K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. Online at http://purl.oclc.org/estimates.

Colwell, R.K. & J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society, Series B 345:101–118.

Colwell, R.K., C.X. Mao & J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85:2717–2727.

Dippenaar-Schoeman, A.S. & R. Jocqué. 1997. African Spiders: An Identification Manual. ARC-Plant Protection Research Institute Handbook, Number 9. Pretoria. 392 pp.

Floren, A. & C. Deeleman-Reinhold. 2005. Diversity of arboreal spiders in primary and disturbed tropical forests. Journal of Arachnology 33:323–333.

Freund, W.M. 2005. Effects of fragmentation and degradation of an afrotropical rain forest on the diversity structure of leaf beetle communities (Coleoptera, Chrysomelidae). PhD thesis, University of Bonn. Online at http://hss.ulb.uni-bonn.de/diss_online/math_nat_fak/2005/freund_wolfram.

Gotelli, N.J. & R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Guilbert, E. 1997. Arthropod biodiversity in the canopy of New Caledonian forests. Pp. 265–277. *In* Canopy Arthropods. (N.E. Stork, J. Adis & R.K. Didham, eds.). Chapman & Hall, London.

Guilbert, E., J. Chazeau & L. Bonnet de Larbogne. 1994. Canopy arthropod diversity of New Caledonian forests sampled by fogging: preliminary results. Memoirs of the Queensland Museum 36:77–85.

- Höfer, H., A.D. Brescovit, J. Adis & W. Paarmann. 1994. The spider fauna of Neotropical tree canopies in Central Amazonia: first results. Studies on Neotropical Fauna and Environment 29:23–32.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.
- Krüger, O. & G.C. McGavin. 1997. The insect fauna of Acacia species in Mkomazi Game Reserve, north-east Tanzania. Ecological Entomology 22:440–444.
- Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell Science Ltd., Oxford, UK. 256 pp.
- Mody, K., H.A. Bardorz & K.E. Linsenmair. 2003. Organization of arthropod assemblages in individual African savanna trees. Pp. 198–212. *In* Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy. (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching, eds.). Cambridge University Press, Cambridge, UK.
- Platnick, N.I. 2008. The World Spider Catalog, Version 8.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html.
- Russell-Smith, A. & N.E. Stork. 1994. Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. Journal of Tropical Ecology 10:545–558.
- Russell-Smith, A. & N.E. Stork. 1995. Composition of spider communities in the canopies of rainforest trees in Borneo. Journal of Tropical Ecology 11:223–235.
- Saaristo, M.I. & A. van Harten. 2002. The oonopid spiders (Arachnida: Araneae: Oonopidae) of Socotra, Yemen. Fauna of Arabia 19:311-319.

- Silva, D. 1996. Species composition and community structure of Peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria river. Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3–8 September 1995. Revue Suisse de Zoologie, vol. hors série:597–610.
- Song, D.X., M.S. Zhu & J. Chen. 1999. The Spiders of China. Hebei Science and Technology Publishing House, Shijiazhuang, Hebei. 640 pp.
- Sørensen, L.L. 2004. Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. Biodiversity and Conservation 13:437–452.
- Ubick, D., P. Paquin, P.E. Cushing, & V. Roth (eds.). 2005. Spiders of North America: an Identification Manual. American Arachnological Society, 377 pp.
- Wagner, T. 1997. The beetle fauna of different tree species in forests of Rwanda and East Zaire. Pp. 169–183. In Canopy Arthropods. (N.E. Stork, J. Adis & R.K. Didham, eds.). Chapman & Hall, London.
- Wagner, T. 2003. Seasonality of canopy beetles in Uganda. Pp. 146–158. *In Arthropods of Tropical Forests*. Spatio-temporal Dynamics and Resource Use in the Canopy. (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching, eds.). Cambridge University Press, Cambridge, UK.
- Walther, B.A. & J.L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28:815–829.

Manuscript received 15 December 2007, revised 21 May 2008.

Appendix 1.—Number of individuals per species at each site.

		1 1	ondin 1.												
	Kakum, Ghana	Luki, DR Congo	Kakamega, Kenya	Mt. Kenya, Kenya	Aberdare, Kenya	Gatamayu, Kenya	Budongo, Uganda	Mt. Elgon, Uganda	Semliki, Uganda	Cyamudongo, Rwanda	Ibanda Makera, Rwanda	Faro, Cameroon	Mkomazi, Tanzania	Comoé, Ivory Coast	Total
Ischnothyreus sp.1	-	1	-	_	-	-	-	-	-	_	-	_	-	_	1
Opopaea sp.1	15	-		-	-	_	_	-	-	_	_	_	-	_	15
Opopaea sp.2	6	-	-	-	_	-	-	-	-	-	-	-	-	-	6
Opopaea sp.3	-	86	-	-	-	-	-	-	-	-	-	-	-	-	86
Opopaea sp.4	-	-	-	18	4	17	-	78	-	-	-	ca ca	•	-	117
Opopaea sp.5	-	-	2	-	-	-	13	-	26	-	3	-	-	-	44
Opopaea sp.6	-	-	-	-	-	-	-		l		a			-	1
Opopaea sp.7	-	-	-	-	-	-	-	-	-	7	-	16	-	12	7 28
<i>Opopaea</i> sp.8 <i>Opopaea</i> sp.9	-	-	3	-	-		-	-	-	-	_	10	_	12	3
Opopaea sp.10	_			-	_	28	_	_	-	_	_	_	_	_	28
Opopaea sp.11	_	_		_	1	6	_	_	_	w	-	_	_	_	7
Opopaea sp.12	-	-	-	12	7	_	_	_	-	-	_			-	19
Opopaea sp.13	-	_	_	6		-	-	-	-	-	-	-	**	-	6
Opopaea sp.14	-	-	-	7		-	-	-	-	-	-	-			7
Opopaea sp.15	-	-	-	-	-	-	-	-	-	-			70		70
Opopaea sp.16	-	-	-	-	-	-	-	-	-	-	-	-	25	-	25
Opopaea sp.17	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Orchestina sp.1	134	-	-	-	-	-	-	-	-	-	-	-	-		134
Orchestina sp.2	91	200	- 02	-	-	-		-	-	~	-		-	en	91 553
Orchestina sp.3	138	308	82	-	-	-	25	-	-	-	-	-	-		553 7
Orchestina sp.4 Orchestina sp.5	7	19	_	-	-	-	-	-	10	-	_	_	_		19
Orchestina sp.6		2	_	_	_		-	_		_			_	_	2
Orchestina sp.7	_	2	-	-	_	_	_	_	_	_	**			-	2
Orchestina sp.8	7	142	1	_	_	-	19	_	_	-	10	-		cor.	169
Orchestina sp.9	-	-	72	_	-	-	-	_	-	2	-	-		-	74
Orchestina sp.10	-	-	-	-	-	-	20	-	-	-	-		-	-	20
Orchestina sp.11	-	-	-	-	-	-	5	-	-	-	-	-	-	-	5
Orchestina sp.12	-	-	-	-	-	-	1	-	-	-			-	-	1
Orchestina sp.13	-	-	-	4	-	14	-	-	-	-	m	-	-		18
Orchestina sp.14	-	-	-	-	-	-	-	-	-	-	•	-	10		10
Orchestina sp.15	-	-	-	-		•	-	-	-	-		-	45 6		45 6
Orchestina sp.16 Orchestina sp.17	-	-	-	-	-	-		-	-		-	228			228
Orchestina sp.18	_	-	_	_		-	_		_	_		7	-		7
Undescr. genus 1 sp.1	œ	a	_			_	_	16	63	œ	-		-		16
Undescr. genus 1 sp.2	68	_	10	_			e	-	2	-	**		-	-	2
Undescr. genus1 sp.3	-	-	1	-	_	ca	6	_	-	-	ю.	œ		-	7
Undescr. genus1 sp.4	-	-	-	12	3	-	-	-	~	-	-		-	-	15
Undescr. genus2 sp.1	-	-	-	-	•	œ	-	-	-	-	1			-	1
Undescr. genus3 sp.1	-	-	-	-	-	-	œ	43	-	-	Ga .		•		43
Undescr. genus3 sp.2	-	**		1	œ	-	-	-	-			-	œ		1
Undescr. genus4 sp.1	52	-	-	-	-		-		-	ω	œ	-		-	52
Undescr. genus4 sp.2	1	23		-	-	-		-	-		-	-	OH.		1 23
Undescr. genus4 sp.3 Undescr. genus5 sp.1	2	23		œ	-		_	-				-	_		2
Undescr. genus5 sp.1 Undescr. genus6 sp.1	2	_	5	-		_	_	_		_	-	_			5
Undescr. genus6 sp.1	-	-	<i>J</i>	-	-		-	_	_	_		-	4		4
Undescr. genus7 sp.1		_	-			-	_	_	_	-		3		100	3
Undescr. genus8 sp.1	26	-	-	-	_		60	_	-	-	_	-		-	26
Total ind.	479	583	166	60	15	65	89	137	29	9	4	254	161	12	2063
No. of species	11	8	7	7	4	4	7	3	3	2	2	4	7	1	51
No. of genera	5	4	4	4	2	2	3	3	2	2	2	3	3	1	11